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The phenology of Collembola from South Central Canada

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With 5 figures

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1. Introduction

In temperate regions the duration of the life history of collembolans usually is two to twelve months (CHRISTIANSEN 1964, HALE 1965, JOOSSE 1969). Springtails from areas with extended periods of subzero temperatures are generally assumed to also have prolonged life histories from one to seven years (BELLINGER 1954, HALE 1967, USHER 1970, BUTCHER *et al.* 1971, ADDISON 1975 & 1981, FJELLBERG 1975, BURN 1981). There is no winter growth or recruitment (STREBEL 1932, ADDISON 1975 & 1981, HUHTA & MIKKONEN 1982). Even in temperate areas no growth is seen during winter (HEALEY 1967, JOOSSE 1969, JOOSSE & VELTKAMP 1970, NIIJIMA 1975, LEINAAS 1983, MERTENS *et al.* 1982). As with all generalities, there are exceptions — *Tetracanthella sylvatica* YOSII and *Isotoma notabilis* (TULLB.) of Japan (TAKEDA 1976, 1978), and subantarctic *Cryptopygus antarcticus* WILLEM [BLOCK 1982] all display some growth and/or development at around 0 °C. Low temperatures may also bring about other phenomena, such as cold resistance (AGRELL 1941, BELLINGER 1954, BUTCHER *et al.* 1971, ZETTEL 1983), and ecomorphosis (CHRISTIANSEN 1964, FJELLBERG 1978a, 1979, ZETTEL 1983). As well, many collembolans are assumed to retreat further into the litter and/or soil to avoid temperature and humidity extremes (AGRELL 1940 & 1941, DRIFT 1951, MILNE 1962, KACZMAREK 1963, CHRISTIANSEN 1964, DOWDY 1965, HALE 1967, ADDISON 1975, TAKEDA 1976, 1978). Thus temperate regions, such as southern Manitoba with strongly continental climate and five to six months of snow cover, seem to show prolonged developmental periods in collembolan species.

The presence of snow cover moderates the microenvironment of the collembolans dramatically (BELLINGER 1954, PERSSON & LOHM 1977, AITCHISON 1978 & 1979, LEINASS 1978 & 1983), so that in southern Canada the subnivean (under the snow) temperature rarely drops below —8 °C (AITCHISON 1978, 1979). The mean annual temperature of southern Manitoba is +2.2 °C, with extremes from —35 °C during winter to +35 °C during summer and with rapid seasonal temperature changes in spring and autumn (Winnipeg Meteorological Office). Consequently the determination of the phenological relationships of collembolan species from such an area should identify those effects related to the climate. Life histories of winter-active spiders are prolonged by the low mean annual temperature (AITCHISON in press).

In this study WINTER is defined as that period of low temperatures with snow cover, November to mid-April; SPRING usually refers to the period of mid-April until the end of May. SUMMER extends from June to the end of August; and AUTUMN is September and October. WINTER-ACTIVE means locomotory activity during winter by any individual of a species at temperatures of 2 °C or lower. The collembolan "life forms" of GISIN (1943), modified by CHRISTIANSEN (1964) and WALLWORK (1970), are used in this study as follows: EUEDAPHIC refers to animals in deep soil layers, with short antennae, very small or no eyes and no pigment, except possibly in the eyes; HEMIEDAPHIC is defined as being in the litter, with moderately long antennae and well-developed pigmentation; and EPEDAPHIC refers to animals on the surface of the litter, with long antennae and eight eyes. LITTER consists of loose, dry leaves and organic matter, while HUMUS is partially decomposed organic matter. RECRUITMENT refers to natality.

The objectives of this study were to ascertain (**1**) the number of generations per year for each collembolan species in south central Canada; (**2**) the size classes of overwintering species; (**3**) the dura-

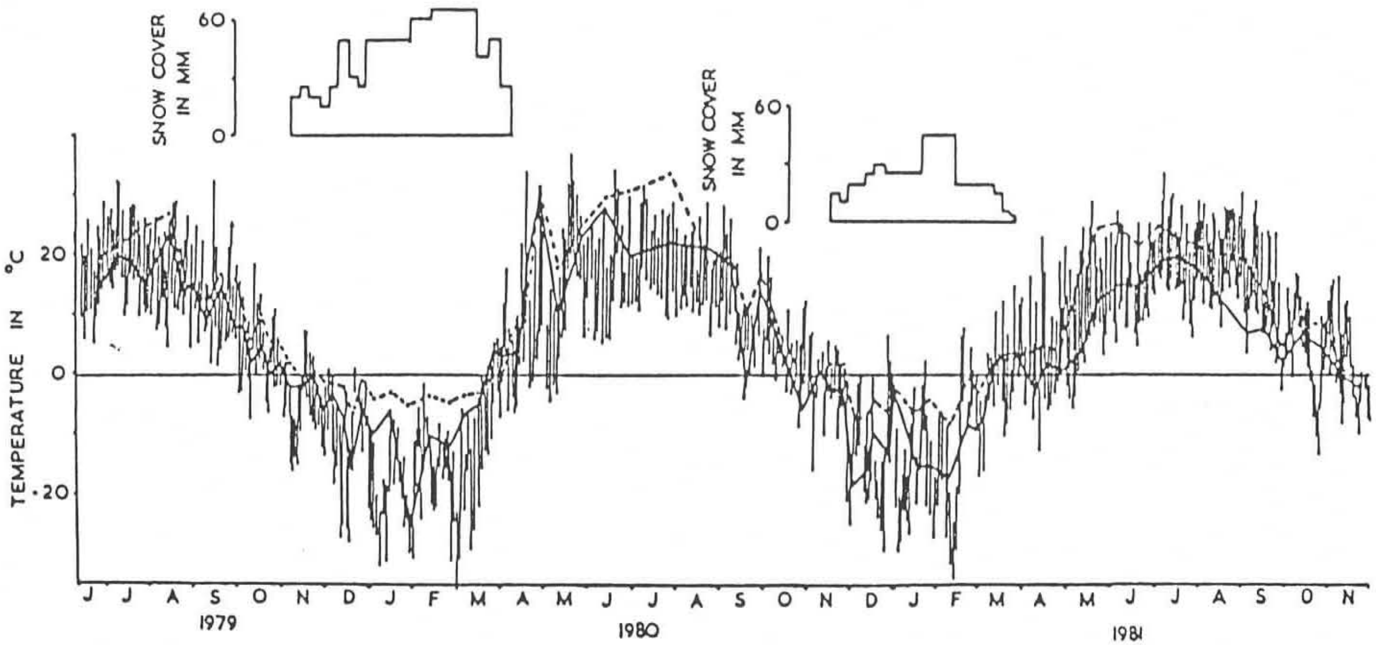

Fig. 1. Meteorological date from June, 1979, to November, 1981, giving the minimum-maximum air temperatures (vertical lines) for every other day, the air temperature at the time of collection (solid line) and the mean soils surface of subnivean temperature (dashed line); in addition the duration of snow cover and its thickness are shown.

tion of the life histories; (4) the winter-active species; (5) the seasonal changes in vertical distribution of these species; and (6) the overwintering sites. Since no similar study has been found in North America at this latitude, this study will add to the information on collembolan life histories.

2. Site and methods

The study site consisted of a mixture of aspen-bur oak woods *(Populus tremuloides-Quercus macrocarpa)* and long grass prairie in the limited access grounds of Canada Cement Lafarge Company, Fort Whyte, Manitoba, Canada (49°49′ N, 97°13′30″ W).

Since pitfall sampling is a good method to study collembolan phenology (JOOSSE 1965), three transects of pitfall traps were established in the study area. One transect of eight traps was located in the wood and another in a small damp meadow, while a third transect of four traps was placed in an ecotone area between the wood and a marshy area. The trap consisted of an inner plastic cup (⌀ 7 cm, height 8 cm) containing a mixture of ethylene glycol and water, within an outer cup (⌀ 8 cm, height 12.5 cm) having its upper lip level with the soil surface. During the winter this was covered by a wooden ring and lid to exclude snow (AITCHISON 1979). Traps were 10 m apart in the wood and in the meadow and 5 m apart in the ecotone area.

Sampling of the pitfall traps was done every two weeks from April, 1979, until the end of October, 1981, except from late autumn until December, and from March until just after snowmelt, when it was done weekly. The thickness of the snow cover, the mean soil surface temperatures and ambient air temperatures (Fig. 1) were noted at the times of collection by radiotelemetric devices and long-stemmed thermometers, using methods described previously (AITCHISON 1978). Specimens were transfered to vials of ethylene glycol with a brush.

Two quadrat samples (25 cm × 25 cm) of litter and two core samples (⌀ 9 cm, depth 5 cm) per site were collected monthly from October, 1980, until October, 1981, and placed in modified Macfadyen funnels (MACFADYEN 1961) for extraction to approximate the seasonal densities of species on the soil surface and in the soil layers. Two layers of soil were sampled, 0—2.5 cm and 2.5—5 cm deep. Sweeping of undergrowth in the meadow and beating of bushes in the wood were also done in snow-free periods. Vacuuming of tree trunks in early and late summer of 1983 produced no specimens, perhaps due to extreme heat and drought.

Samples were run through a coarse filter, washed with distilled water, specimens stored in 70% ethanol and identified to species level if possible. K. A. CHRISTIANSEN (Grinnell, U.S.A.), A. FJELLBERG (Tromsø, Norway), M. M. GAMA F. ASSALINO (Coimbra, Portugal) and R. J. SNIDER (East Lansing, U.S.A.) identified specimens difficult to determine. The total body length, excluding antennae, of each individual was measured in mm (± 0.15 mm). The length of curved specimens was estimated as if the body were straight. Since ethanol fixation of *Isotoma viridis* BOURLET causes a 21.1% extension of body length (MERTENS pers. comm.), all measurements were corrected to the length of the live individual. All other species are thus calculated at this maximum length, although extension varies with species and fixative (MERTENS et al. 1982, pers. comm.). In each species the size classes (1—10) were determined by the difference between the largest and smallest individuals seen divided by ten, and the proportion of specimens in each size class was used as an indirect measure of field population growth for life history determination (HUHTA & MIKKONEN 1982). The separation of generations is not as easily discernible in a horizontal polymodal frequency distribution as in a vertical table displaying the numbers of each size class at different times (STRAALEN in press). In such a table, considerable changes in the numbers of a size class over time indicate new generations.

Laboratory cultures were maintained at 10, 15 and 20 °C of some more common species: *Hypogastrura denticulata* (BAGNALL) complex, *Onychiurus pseudoarmatus* FOLSOM, *Proisotoma minuta* (TULLBERG), *I. viridis*, *Orchesella ainslei* FOLSOM, *Entomobrya gisini* CHRISTIANSEN, *Lepidocyrtus violaceus* FOURCROY and *Tomocerus flavescens* TULLBERG. The minimum and maximum size of each species were noted.

3. Results

3.1. General phenology

Information on each collembolan species about life form, habitat, size range of the species, the number of generations per year, the months with young appearing, winter-activity, and the overwintering size classes is given in Table 1. Additional knowledge on the same species from the literature is noted.

For the twelve arthropleone species in which it was possible to determine the number of generations per year, five species — *Hypogastrura sp.*, *I. viridis*, *Folsomia elongata* (MAC GILLIVRAY), *Entomobrya gisini* CHRISTIANSEN, and *Tomocerus flavescens* — were bivoltine (41.7%), *O. ainslei* had two to three generations per year (8.25%); *Isotomurus palustroides* FOLSOM and *Entomobrya purpurascens* (PACKARD) had three generations per year (16.7%),

Table 1. Information on the life histories of various species of Collembola

Species	Life form	Habitat	Size in mm	Genera-tions/year	Months with young	Winter activity	Overwinter size class	Reference
Hypogastruridae								
1) *Hypogastrura denticulata* (BAGNALL) complex	hem	meadow, wood	0.25—1.45	3—5	IV, VII, VIII, IX, X	slight	1—4	this study
2) *Xenylla sp.*, poss. *louisiana* GAMA	hem	meadow				no		this study
3) *Neanura muscorum* TEMPLETON	hem	wood	0.9—1.5			no		this study
	hem							GISIN 1943
		litter, upper soil						BELLINGER 1954
								BÖDVARSSON 1973
	ep							MILNE 1960
Onychiuridae								
4) *Onychiurus pseudoarmatus* FOLSOM	eu	meadow	0.5—1.4	3—4	IV, V, VII, IX	yes	2—5	this study
Isotomidae								
5) *Proisotoma clavipila* AXELSON	eu?	wood	0.66*			?		this study
6) *Proisotoma minuta* (TULLBERG)	hem-eu	wood, meadow	0.3—1.1	3—4	IV, VI, VII, X	yes	2—6	this study
	hem							GISIN 1943
				2 (UK)				HUTSON 1981
7) *Folsomia elongata* (MACGILLIVRAY)	hem	wood, meadow	2	VI, X	no?	0.74 to 2.07 mm		this study
		litter, top 5 cm of soil						DOWDY 1965
8) *Folsomia fimetaria* (L) *s. l.*	eu	wood, meadow	0.33—1.0			no		this study
	eu							GISIN 1943
		litter, top 5 cm of soil						DOWDY 1943
				VIII, XI				PERSSON & LOHM 1977
9) *Folsomia nivalis* (PACKARD)	eu							this study

10) *Isotomurus palustroides* FOLSOM	hem	wood, meadow	0.41—1.81	3	IV, VII, IX	no	1—8	this study
11) *Isotoma blufusata* FJELLBERG	hem	meadow, ecotone	1.0—1.24			yes		this study
12) *Isotoma fennica* REUTER	hem	litter	0.83*			yes yes		this study FJELBERG 1979
13) *Isotoma manitobae* FJELLBERG	hem	wood, litter	0.83—1.0			yes		this study
14) *Isotoma notabilis* SCHÄFFER	eu	meadow				no		this study
	eu	forest humus, top 3 cm of soil						BÖDVARSSEN 1973 PETERSEN 1980
				1 (N)	VI-VII			FJELLBERG 1975
				2 (n S)	VI-VII			AGRELL 1941
				3 (S)	III, VI, VII			BÖDVARSSEN 1973
				4 (DK)				HAARLØV 1960
15) *Isotoma sp. (propinqua* AXELSON gr.)	hem	litter						this study
16) *Isotoma quadra* CHRISTIANSEN & BELLINGER	hem	wood					yes	this study
17) *Isotoma subviridis* FOLSOM gr.	hem	meadow, litter					yes	this study
18) *Isotoma viridis* BOURLET gr., s.l.	hem	meadow, wood	0.4—3.84	2	V, X	yes	1—5	this study
	ep-hem	litter, top 3 cm of soil, tree trunks						GISIN 1943 WEIS-FOGH 1948 HAARLØV 1960 MILNE 1962 DOWDY 1965 BÖDVARSSEN 1973 PERSSON & LOHM 1977
			1 (N)					FJELLBERG 1975
			2 (UK, NL)	autumn, spring	yes			MILNE 1962 JOOSSE 1969 USHER 1970 HUTSON 1981

Table 1 Continued.

Species	Life form	Habitat	Size in mm	Generations/year	Months with young	Winter activity	Overwinter size class	Reference
Entomobryidae								
19) *Orchesella ainslei* FOLSOM	ep-hem	meadow, wood	0.5—2.18 2.18	2—3	V, VI, IX	yes	1—8	this study
		litter, top 5 cm of soil						DOWDY 1965
20) *Orchesella* sp.	ep					?		this study
21) *Entomobrya confusa* CHRISTIANSEN	ep					?		this study
22) *Entomobrya gisini* CHRISTIANSEN	ep	meadow, wood	0.5—2.8	2	V, VII, IX	yes	0.75 to 1.65 mm	this study
23) *Entomobrya nivalis* (L.)	hem	litter				?		this study
	hem			1	VII (CH)			ALLMEN & ZETTEL 1982
				2	VI, X (NL)			JOOSSE 1969
24) *Entomobrya purpurascens* (PACKARD)	hem	wood, meadow	0.41—1.71	3	V, VII, IX	no	6, 7	this study
		litter, top 5 cm of soil						DOWDY 1965
25) *Lepidocyrtus violaceus* FOURCROY	hem	wood, meadow	0.25—1.94	3—4	IV, VII, VII, IX	yes	1—4	this study
26) *Pseudosinella violenta* (FOLSOM)			1.0*		VI	no?		this study
27) *Tomocerus flavescens* TULLBERG	ep	wood, meadow	0.5—3.65	2	IV, VI, VIII	yes	2—8	this study
	hem	litter, humus					juveniles	GISIN 1943 BELLINGER 1954 KNIGHT 1963
				1 (S, US, DK)				AGRELL 1941 BELLINGER 1954 PETERSEN 1980
				1—2 (SF)				HUHTA & MIKKONEN 1982

The abbreviations are: ep = epedaphic, hem = hemiedaphic, eu = eudaphic; CH = Switzerland, DK = Denmark, N = Norway, NL = The Netherlands, S = Sweden, SF = Finland, UK = United Kingdom and US = United States. The asterisk represents only a few specimens.

and another four species, *H. denticulata*, *O. pseudoarmatus*, *P. minuta* and *L. violaceus*, had three to four (33.3 %). Seven winter-active species had a mean of 2.64 generations per year, while the four winter-inactive species had a mean of 3.0. If an individual overwintered, its life history could last for up to ten months, but most other individuals probably only live about three months.

3.2. Population density and activity

Each species in the three families is discussed in the section below. First the population densities are considered and then the activity indices. Density is the number of animals per m² at a given time, and activity refers to locomotion and may be defined by an activity index (AI), all in the same time period (With & Joosse 1971), where

$$\mathrm{AI} = \frac{\text{the number of animals in traps}}{\text{population density from soil samples}}$$

Hypogastruridae: *H. denticulata* fluctuated widely in numbers, being most numerous in the meadow. Recruitment was indicated in April and May, early July and late September-early October (Fig. 2a), as concluded from the data in Table 2. The high numbers found in January, October and November are probably caused by the hatching of eggs in the extraction funnels, since many small individuals were extracted. The highest AI occurred between August and October (Fig. 2a). Also the tendency to aggregate may have biased the results in estimating seasonal density.

Onychiuridae: *O. pseudoarmatus* had low numbers in March, August and December and peaks in May, October to November in the meadow, suggestive of recruitment of juve-

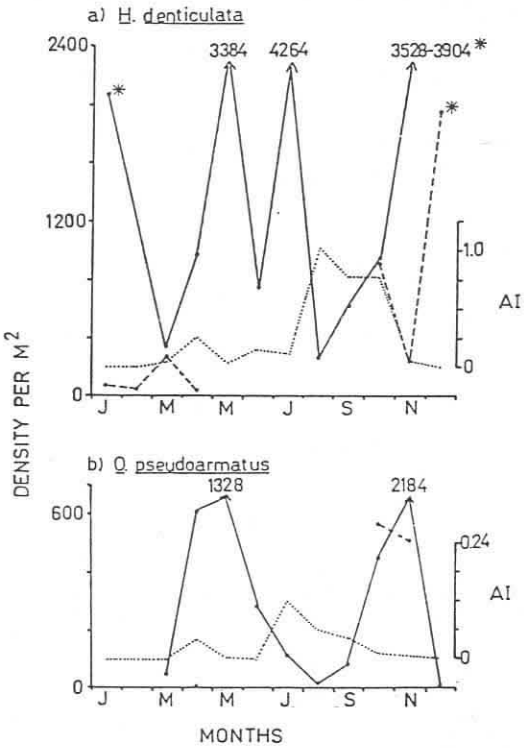

Fig. 2. The seasonal population densities per m² in the wood (dashed line) and the meadow (solid line), and activity indices (AI; dotted line), showing relative seasonal activity, for a) *H. denticulata* and b) *O. pseudoarmatus* over one year. The asterisks represent young hatched in the extraction funnels.

Table 2. The seasonal frequency distribution of size classes of *H. denticulata* over a period of 19 months (50 sampling units)

Date	Size class 1	2	3	4	5	6	7	8
16 IV 1980		2	1					
30 IV								
14 V		1	2	1				
28 V		3	1					
11 VI		2						
25 VI	8	23	6	1	2			
24 VII	2	6	10	3	9			
20 VIII	13	57	56	9	35	6	3	1
4 IX	28	79	74	15	33	6	1	
17 IX	59	147	105	31	74	16		
1 X	5	22	12	4	10	1	1	
15 X	1	5	14	2	3	3	1	
29 X		6	3	1				
XI	1	5	2					
XII	(7)	4 (16)	(1)					
I 1981		1						
II								
III		1						
8 IV	17	99	88	17	17	5		
23 IV	16	81	64	14	34	9		2
6 V	31	63	37	10	24	6	1	
20 V	25	55	18	2	3			
3 VI	18	57	51	14	27	5	4	
17 VI	17	146	279	102	245	52	9	
2 VII	92	350	215	54	285	57	5	
14 VII	610	497	214	66	145	46	6	
27 VII	112	133	98	34	79	22	2	1
4 IX	46	189	256	78	143	26	3	1
16 IX	28	68	79	17	39	13	2	
28 IX	107	226	274	78	142	27	1	
12 X	65	120	109	49	79	22	2	
29 X	127	125	29	3	2			

Note: Stepwise lines delinate generations, blanks indicate zeroes, and numbers in parentheses indicate specimens extracted from litter and the others specimens from pitfall catches. Size class 1 begins at 0.25 mm, and each class adds another 0.15 mm.

niles (Fig. 2b), while Table 3 suggests further recruitment. The highest AI were in July and August. This species also aggregates.

Isotomidae: *P. minuta* showed low densities in April and August and high densities in March, June and July, and September—October. The peak in March is possibly caused by hatching of eggs. Recruitment of juveniles appears to occur in June—July and September to October (Fig. 3a and Table 4), although the table indicates one or two more periods of recruitment. Individuals of this species aggregate. The highest AI occurred in August.

Folsomia fimetaria (LINNAEUS) from the meadow exhibited a small peak in May and a high one in November, suggestive of recruitment twice a year, April and October. Possibly this species occurs in aggregations (Fig. 3b). It always had an AI of zero, indicating a sedentary life style.

I. viridis had peaks in density February and March (probably from hatched eggs), June and a small one in November, suggesting recruitment in April—May and November and corroborated by Table 6 (Fig. 3c). The AI were high in January, May, and July—August.

Entomobryidae: *O. ainslei* from the meadow exhibited low population densities in January, June and October and high ones in February to May and August, suggesting

Table 3. The seasonal frequency distribution of size classes of *O. pseudoarmatus* over a period of 19 months (50 sampling units)

Date	Size class 1	2	3	4	5	6	7	8
I								
II				3				
III			1		1			
15 IV		3	6	8	5	1		
30 IV					2			
15 V						1		
30 V								
15 VI		4		1				
30 VI		8	2	18	4	5		
15 VII			4	6	4			
30 VII		5	5	25	11	4		
15 VIII					1			
30 VIII		1		5	1			
15 IX		2	1	2	1			
30 IX		1		3	1	1		
15 X			1	10	6			
30 X			1	4	1	1		
XI			2	8				
XII					1			

Note: Stepwise lines delineate generations, blanks indicate zeroes. Size class 1 begins at 0.50 mm, and each class adds another 0.13 mm.

Table 4. The seasonal frequency distribution of size classes of *P. minuta* over a period of 12 months (32 sampling units)

Date	Size class 1	2	3	4	5	6	7	8
IX 1980		2	14	23	21	3		
XII		1	1	2	3			
I 1981								
II					1	1		
III			2	2	1	2		
8 IV			3	2	4			
23 IV		2	2	6	10	2		
6 V		2	5	16	10	1		
20 V		1	4	9	3			
3 VI				1	2			
17 VI			2	6	9	2		
2 VII	1	1	3	6	1	2	3	
14 VII	8	47	80	47	23	5	1	1
27 VII		7	11	6	1	2		
4 IX	1							
16 IX		2	2			1		
28 IX		2	4					1
12 X		2	1	1	1			
29 X		4	5	5				

Note: Step-wise lines delineate generations, blanks indicate zeroes. Size class 1 begins at 0.3 mm, and each class adds another 0.1 mm.

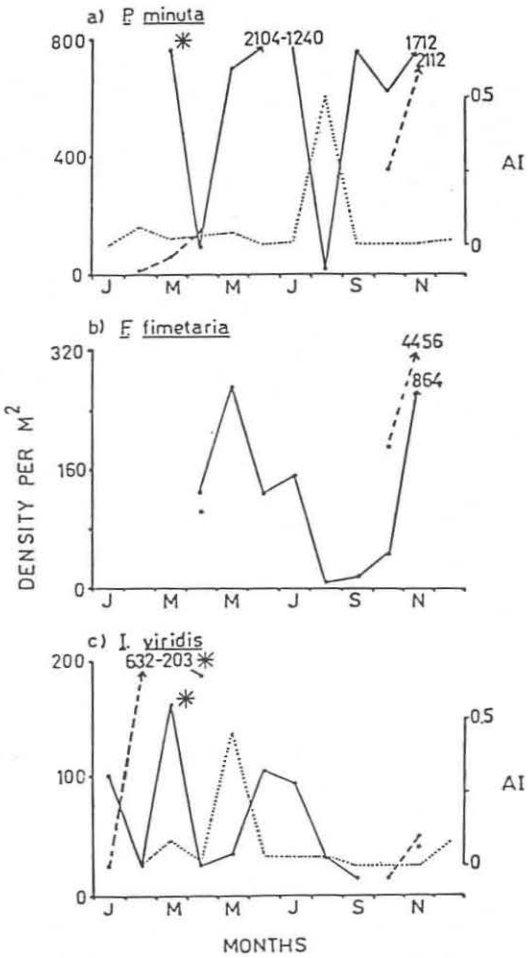

Fig. 3. The seasonal population densities per m² in the wood (dashedl ine) and in the meadow (solid line), and activity indices (AI) (dotted line) for (a) *P. minuta*, (b) *F. fimetaria* and (c) *I. viridis* over one year. The asterisks represent young hatched in the extraction funnels.

Table 5. The seasonal frequency distribution of size classes of *I. palustroides* over a period of 19 months (50 sampling units)

Date	Size class							
	1	2	3	4	5	6	7	8
I								
II								
III								
IV		1		1				
V		1			1	1	1	1
VI				1			1	
VII		2	1	1		1	1	3
VIII								
IX	1	1	3	1			1	1
X								
XI								
XII								

Note: Stepwise lines delineate generations, and blanks indicate zeroes. Size class 1 starts at 0.41 mm, and each class adds another 0.24 mm.

Table 6. The seasonal frequency distribution of size classes of *I. viridis* over a period of 19 months (50 sampling units)

Date	Size class							
	1	2	3	4	5	6	7	8
I 1980								
II						1		
III				2				
16 IV		2		1				
30 IV	14	4	4	1	3			
14 V	1	6	1	3				
28 V		5	2	2	1			
11 VI		5	1	1				
25 VI		2	1					
24 VII	1	8	1		1			
20 VIII	2	4	4					
4 IX	1	10	10	1		1		
17 IX	1	9	2	1				
1 X		1						
15 X	3	4	3	6				
29 X			1	4	3			
XI		1		1	3			
XII	(7)	1 (8)	(1)	10 (1)	4 (1)			
I 1981	1	2	2	1	3			
II		2	3		2			
III		1		2				
8 IV	1		2		2	2		
23 IV		1	6	1	8			
6 V	6	4	7	7	11	2		
20 V		1	1	3	7	3	1	
3 VI	1		1	3	1			
17 VI		5	11	8	1	1		
2 VII	1	13	19	6	1	1		
14 VII	2	9	30	19	8	1		
27 VII	2	10	7	5	1			
4 IX	2	5	5	1	1			
16 IX	3	10						
28 IX	1	12	10					
12 X		3	9	1				
29 X	1	2	9	2				

Note: Step-wise lines delineate generations, blanks indicate zeroes, and numbers in parentheses indicate extracted specimens. Size class 1 starts at 0.40 mm, and each class adds another 0.43 mm. In XI 1980 and in II 1981 individuals were seen on snow.

recruitment in April—May and August (Fig. 4a), while Table 7 suggests another recruitment period in mid-June. The AI rose in May, to a high in July—August, followed by a decrease in September and another high (2.38) in October in the wood (Fig. 4a).

L. violaceus from the wood had low densities in January, March and October and high ones in February (probably from egg hatch), April and December (from egg hatch), while in the meadow recruitment was indicated in April (Fig. 4b); Table 8 shows recruitment in July as well. The AI increase from May to a maximum in August (2.13); otherwise they are low except for minor activity in January and November (AI = 0.13 in both instances).

3.3. Seasonal changes in vertical distribution

Core samples were extracted to determine if seasonal variation in vertical distribution occurs. The low number of cores (two per habitat per month) probably underestimates some populations, especially in those species which aggregate. The percentage of those species in the lower layer (2.5—5 cm) of soil are presented in Figure 5.

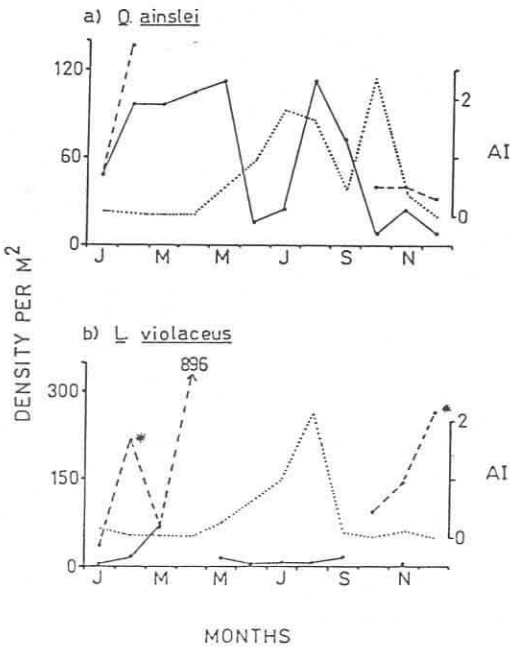

Fig. 4. The seasonal population densities per m² in the wood (dashed line) and in the meadow (solid line), and the activity indices (AI) (dotted line) for (a) *O. ainslei* and (b) *L. violaceus* over one year. The asterisks represent young hatched in the extraction funnels.

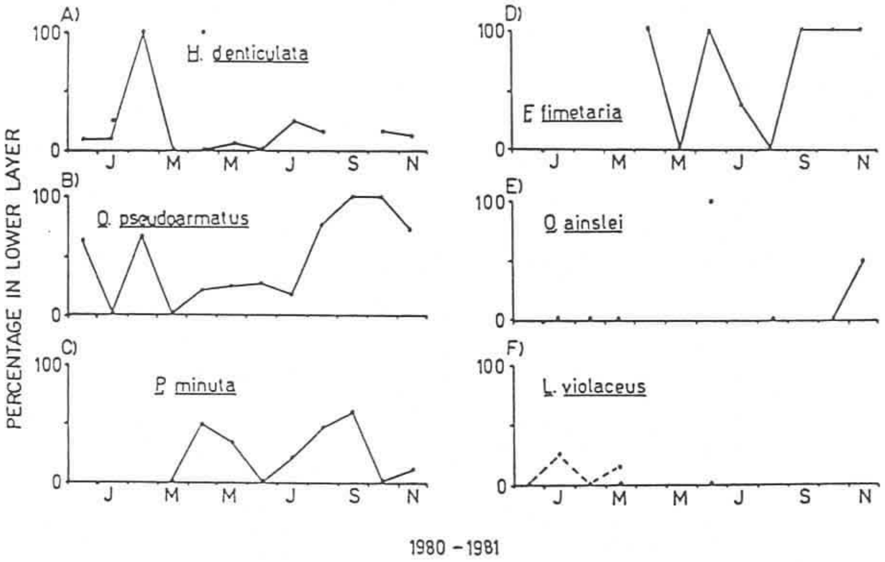

Fig. 5. The percentages of (A) *H. denticulata*, (B) *O. pseudoarmatus*, (C) *P. minuta*, (D) *F. fimetaria*, (E) *O. ainslei* and (F) *L. violaceus* collected each month in the lower soil layer. The dashed line represents the percentages in the wood, and the solid one those in the meadow.

Table 7. The seasonal frequency distribution of size classes of *O. ainslei* over a period of 19 months 50 sampling units)

Date	Size class							
	1	2	3	4	5	6	7	8
I 1980		2	4	5		1		
II			2	3				
III	1	4	5	7	2			
16 IV	3	8	13	20	10	5		
30 IV		10	9	56	17	5		
14 V		11	25	55	34	11	1	
28 V		2	7	14	6	4		1
11 VI	1	2	7	34	12	7		
25 VI	3	5	10	59	24	12		
24 VII	7	13	28	39	19	5		
20 VIII	6	10	17	39	12	5		
4 IX	3	18	40	49	15	2		
17 IX	9	49	40	56	11	5		
1 X	5	9	7	16				
15 X	1	11	6	12	4	2		
29 X	3	6	1	2	2	2		
XI	1	1	1		1			
XII	3	6	11	16	4	4		
I 1981	1	2	8	14	6			1
II	3	13	14	13	6	3		
III	1	7	6	6	2	1		
8 IV	1	7	5	13	11	2	1	
23 IV	1	10	9	42	18	6		
6 V		20	33	103	70	41		2
20 V		16	42	154	76	34		
3 VI			6	18	21	14		
17 VI	6	3	5	77	39	21		
2 VII	25	16	9	27	23	13		
14 VII	117	214	103	96	50	27		
27 VII	105	347	196	169	31	17	1	
4 IX	11	26	41	25	2	3	1	
16 IX	27	45	37	27	4	3		
28 IX	5	38	28	29	2			
12 X		8	7	8				
29 X	3	4	7	7				

Note: Step-wise lines delineate generations, and blanks indicate zeroes. Size class 1 begins at 0.50 mm and each class adds another 0.21 mm.

Hypogastruridae: In the meadow the hemiedaphic species, *H. denticulata*, was found in the lower soil layer in all months except March, April and June. The September samples contained no specimens of this species. Generally small juveniles were encountered; in February all representatives of this species were found in the lower soil layer (Fig. 5a).

Onychiuridae: Again in the meadow the eudedaphic species, *O. pseudoarmatus*, occurred in the lower layer all months except January and March, although a high proportion of individuals were found in the cooler months of September through December and in February (Fig. 5b). This species probably is always in the lower layer; the small number of samples and the species' aggregation probably resulted in no specimens being found in some months.

Isotomidae: The hemi-euedaphic species, *P. minuta*, was in the lower layer of the meadow in April—May, July—September and November (Fig. 5c). Euedaphic *F. fimetaria* was found in the lower layer of meadow soil from April to November. None were collected in May or August. These exceptions probably are due to the number of samples (Fig. 5d). The small euedaphic species, *Folsomia nivalis* (Packard), was encountered once in the lower

Table 8. The seasonal frequency distribution of size classes of *L. violaceus* over a period of 19 months (50 sampling units)

Date	Size class 1	2	3	4	5	6	7	8
I—III 1980								
16 IV								
30 IV						3		
14 V		1		4	1	1		
28 V						1		
11 VI			1	12	8	7		
25 VI				1	4	1		
24 VII				1	2			
20 VIII				1	1			
4 IX		3	1	7	1			
17 IX		1	3	2	2	1		
1 X		1	2	1		1		
15 X				2	1			
29 X		2	2	2				
XI		6	1	1				
XII	(16)	(82)	(41)	2 (12)				
I 1981	1	1		1				
II	3	9	8	2				
III	1	13	2					
8 IV			4	1				
23 IV		2	3	2				
6 V	1	14	26	20	4	1		
20 V		14	38	29	2			
3 VI		1	7	8		1	1	
17 VI		2	10	28	5			
2 VII		8	7	20	8			
14 VII	1	63	82	48	9	1		
27 VII	9	90	118	82	6			
4 IX	1	8	21	5				
16 IX	5	32	11	3				
28 IX		13	11	1				
12 X	1	10	11	5				
29 X	1	9	4					

Note: Step-wise lines delineate generations, blanks indicate zeroes, and numbers in parentheses indicate extracted specimens. Size class 1 begins at 0.25 mm, and each class adds another 0.21 mm.

layer of the meadow soil in December, as was the small euedaphic *Isotoma notabilis* SCHAFFER. *I. viridis*, a large hemiedaphic species, was never found in the lower layer of the meadow soil.

Entomobryidae: One small juvenile of *O. ainslei*, a medium-sized ep-hemiedaphic collembolan, was seen in the lower soil layer in June (Fig. 5e). *L. violaceus*, a smaller hemiedaphic species, was never found in the lower layer of meadow soil, while a few individuals were collected at that level in the wood in January and also in March (Fig. 5f). Possibly there is some downwards migration by a few juveniles of these species during environmental extremes.

4. Discussion

4.1. General phenology

The climate of Manitoba does not prolong collembolan life cycles, although it does in spiders. The life histories of collembolans are like those of southern England and mid-Europe. By contrast, the duration of spider life histories in Manitoba is similar to that in northern Sweden (AITCHISON in press). The variation in the number of generations per year was shown

Table 9. The seasonal frequency distribution of size classes of *T. flavescens* over a period of 19 months (50 sampling units).

Date	Size class							
	1	2	3	4	5	6	7	8
I 1980		1	1	3				
II					3			
III		1	2	1				
16 IV		1		2	11			
30 IV	1	8	13	10	6	2	1	
14 V		1	36	16	8			
28 V		1	8	7	1			
11 VI		1	4	2	5			
25 VI	1		2	3	2			
24 VII			1	3	2			
20 VIII					4	1		
4 IX	2	1	2	7	7	8	2	
17 IX	1	1	1	8	1	6	4	2
1 X					4	9	7	1
15 X				2	14	15	14	6
29 X				2	6	9	3	1
XI		1		1	10	5	6	1
XII			3	4	7			
I 1981			1		2			
II				1				
III								
8 IV				2				
23 IV			5	1	1	2		
6 V		1	6	3	5	3	2	1
20 V			1	12	7	3		
3 VI			1	6	5	3	2	1
17 VI				3		6	6	
2 VII		4		4	4	3		
14 VII		1	10	9	17	30	10	1
27 VII		2	11	11	47	33	3	1
4 IX			1	2	4	21	27	21
16 IX		2	2	5		5	14	12
28 IX		1	4	4	7	13	37	37
12 X			2	5	2	12	30	24
29 X			1	8	15	13	16	18

Note: Step-wise lines delineate generations, and blanks indicate zeroes. Size class 1 begins at 0.50 mm, and each class adds another 0.35 mm. Dashed lines indicate the time when larger individuals probably move to the soil surface in response to low temperatures.

in *Folsomia quadrioculata* (TULLB.) (with two generations per year in Lapland and northern England (AGRELL 1941, USHER 1970), and three to four in Denmark and Sweden (HAARLOV 1960, BÖDVARSSON 1973), and latitudinal gradation in *I. notabilis* (two generations per year in Lapland (AGRELL 1941), three in Sweden (BÖDVARSSON 1973) and four in Denmark (HAARLOV 1960). In all examples these species reproduce whenever conditions permit, with periodicity governed by the 'livsrythm' of each species (AGRELL 1940). Thus the widely-fluctuating climatic extremes of Manitoba are not detrimental to the collembolans with respect to conditions for development, with an ameliorated microclimate under the snow cover. This is apparent in the number of bivoltine species (five) as compared to the number of multivoltine species (eight), which would be expected in areas with optimal reproductive conditions.

The number of generations per year in the genera or species from southern England, the lowland countries or Japan agree well with those of Manitoban species, as seen in *H. denticulata* [HALE 1965], *I. viridis* [MILNE 1962, JOOSSE 1969, USHER 1970, HUTSON 1981, MERTENS pers. comn.], *Orchesella spp.* [JOOSSE 1969, MERTENS *et al.* 1982, STRAALEN in press]

Entomobrya spp. [JOOSSE 1969], and *Tomocerus spp.* [JOOSSE 1969, TAKEDA 1979, STRAALEN in press].

Probably many collembolans from Manitoba can develop at low temperatures, especially *P. minuta* whose juveniles first appear in early April, just as snow melts and before any juveniles of other species are found. Eggs of this species hatched at 2 °C in the laboratory, and a few specimens moulted at —2 °C. Developmental thresholds between 0 and 5 °C have been documented for *H. denticulata* [THIBAUD 1970], *Onychiurus procampatus* GISIN [HALE 1965], *I. notabilis* [SHARMA & KEVAN 1963], *I. viridis* [HALE 1965], *Orchesella cincta* (L.) [JOOSSE & VELTKAMP 1970), *Entomobrya nivalis* (L.) [ALLMEN & ZETTEL 1983] and *Tomocerus minor* (LUBB.) [HALE 1965, JOOSSE & VELTKAMP 1970].

Generally reproduction of collembolans occurs either in spring or in autumn (MILNE 1962, HALE 1965, HEALEY 1967, JOOSSE 1969, PERSSON & LOHM 1977, HUTSON 1981, MERTENS *et al.* 1982, STRAALEN in press), and in multivoltine populations summer reproduction is also recorded (HAARLØV 1960, TAKEDA 1979). In Manitoba, spring and autumn reproduction were commonly seen, sometimes with a further one to two generations appearing in the summer.

Perhaps a minor change in technique would have increased the number of collembolans. The use of small pitfall traps (⌀ 14 mm) collected more newly-hatched individuals of *I. viridis* in early spring than did larger traps (⌀ 10 cm) (MERTENS pers. comm.). Certainly the small size classes seemed to be underrepresented in the pitfall catch.

Many researchers have noted all size classes, or in particular subadults, overwintering (AGRELL 1940, HAARLØV 1960, KNIGHT 1963, JOOSSE 1969, ADDISON 1977 and 1981, Aitchison 1979, ALLMEN & ZETTEL 1982, BLOCK 1982). In central, southern Canada the majority of winter-active springtails and specimens extracted from quadrat samples were subadults; few large adults were collected over the winter period.

The duration of the life history of Manitoban collembolans is approximately two to ten months, depending on the month in which eggs hatch, as found by CHRISTIANSEN (1964) and by WILLARD (1973). Those individuals which hatch in the autumn have an extended juvenile period throughout the winter. Also small species, such as *P. minuta*, have extremely short life cycles. These estimates, from two to ten months, include those suggested elsewhere of three to six months (HAARLØV 1960, HALE 1965, JOOSSE 1969).

4.2. Population density and activity

Populations of all species of collembolans are highest from April to November after recruitment has occurred (WEIS-FOGH 1948, HALE 1965, JOOSSE 1969, USHER 1970, FJELLBERG 1975, NIIJIMA 1975, PERSSON & LOHM 1977, HUTSON 1981, MERTENS *et al.* 1982). This was confirmed in this study. High numbers of Collembola in temperate regions appear in spring and late summer (DRIFT 1951), also producing high autumn numbers (HAARLØV 1960). In Manitoba maximum numbers occurred in spring, summer and autumn. However some species exhibited high population peaks in midwinter which seemed anomalous, as in *I. notabilis* and *Lepidocyrtus lanuginosus* (GMELIN) of Sweden in February (BÖDVARSSON 1973). LEINAAS (1983) and MERTENS (pers. comm.) have noted high densities of *Lepidocyrtus lignorum* (FABR.) and *I. viridis* respectively in midwinter, probably due to the hatching of overwintering eggs in the extraction funnels. In this study there were extremely high figures for winter densities noted in December and January for *H. denticulata* (Fig. 2a), in March for *P. minuta* (Fig. 3a), in February for *I. viridis* (Fig. 3c) and in December for *L. violaceus* (Fig. 4b), compared to figures for the rest of the winter. Hatching of eggs is suspected because of the large number of small juveniles present at those times. Increased extraction efficiency from frozen soils was noted by several researchers (HEALEY 1967, PERSSON & LOHM 1977, LEINAAS 1978) and may partially explain the higher numbers from winter samples.

Winter densities often decrease by half, especially from mortality of adults (JOOSSE 1969), and certainly specimens of only a few overwintering species were larger than size class 8.

The activity index (AI) was low during winter, or nonexistent in species with little or no winter activity, compared to winter-active *I. viridis* and *L. violaceus* with AIs of 0.31 and 0.13 respectively in January. In spring and autumn prior to recruitment of the next cohorts when densities were low, the AI was generally high (Joosse 1969), probably a result of reproductive activity by the adults (Figs. 2, 3a and c). For many species, the activity indices were greatest when densities were the lowest (Figs. 2, 3a and c, 4), while at times of peaks in density the indices were low.

Winter activity, on or under snow, has been noted in *Hypogastrura nivicola* Fitch [Bellinger 1954], and *H. socialis* (Uzel) [MacNamara 1924, Leinaas 1983], *O. pseudoarmatus*, *Isotoma blufusata* Fjellberg and *Isotoma manitobae* Fjellberg [Aitchison 1979], *Isotomurus palustris* (Müller) (Joosse 1969), *Isotoma fennica* Reuter (Fjellberg 1979], *Isotoma hiemalis* Schött [Zettel 1983], *Isotoma saltans* (Nicolet) [Schaller 1962], *I. viridis* [Joosse 1969, Aitchison 1979], *O. ainslei*, *L. violaceus*, and *Tomocerus flavescens* Tullberg (Aitchison 1979), *I. minor* (Usher 1970) and *Entomobrya multifasciata* (Tullb.) [Persson pers. comm.], previously called *E. nivalis* (L.) [Persson & Lohm 1977). Eight of these fifteen species occur in Manitoba. This study documents winter activity of four more species, indicating that a variety of species exhibit winter activity.

4.3. Seasonal changes in vertical distribution

Downward migration by collembolans of small sizes, whether small euedaphic species or juveniles of hemiedaphic species, happens in response to environmental extremes of temperature and humidity (Agrell 1941, Drift 1951, Milne 1962, Kaczmarek 1963, Sharma & Kevan 1963, Usher 1970, Persson & Lohm 1977). The eudedaphic species, *O. pseudoarmatus*, *F. minuta* and *F. fimetaria*, were commonly found in the bottom of the core sample (2.5—5 cm deep), while the hemiedaphic species such as *I. viridis*, *O. ainslei* and *L. violaceus* were never or rarely found at that depth. There was only slight downward migration by juveniles of *O. ainslei* and *L. violaceus* in periods of very low temperatures.

By contrast some of the entomobryids, *E. gisini* in particular, migrate up into tall bushes during summer months, while *O. ainslei* and *T. flavescens* are often seen on tall grasses. The association of *Orchesella flavescens* (Bourl.), *Entomobrya marginata* (Tullb.) and *E. nivalis* with trees and other large plants is well known (Gisin 1943, Allmen & Zettel 1982, Huhta & Mikkonen 1982, Mertens *et al.* 1982).

Comparison of these findings and those of other researchers generally agree on where species are usually found (Gisin 1943, Weis-Fogh 1948, Drift 1951, Haarløv 1960, Knight 1963, Dowdy 1965, Bödvarsson 1973, Petersen 1980). The sites in which species overwinter appear to be those layers where they are found in frost-free months, with the exception of some downward migration by small juveniles during periods of environmental extremes; these findings corroborate those of Drift (1951) and Dowdy (1965) who documented that most collembolans overwinter in the litter near the soil surface.

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Synopsis: *Original scientific paper*

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Despite the severe continental climate of south central Canada, the eleven species of collembolans had a mean of 2.91 generations per year, with no winter growth or recruitment seen. The duration of life history ranged between two and ten months. Twelve of twenty-seven species are known to be winter-active. Population densities varied seasonally; recruitment usually occurred in spring, summer and autumn. Activity indices were highest in periods of lowest population densities, just prior to recruitment. The highest activity indices during winter were seen in the winter-active species, while the lowest values were found in the euedaphic species. Collembolans usually overwintered in the same layers in which they were found in frost-free months, with some downward migration by juveniles of some hemiedaphic species.

Key words: phenology, life cycle, life history, Collembola, springtail, winter-active, winter, Manitoba Canada.